RESEARCH ARTICLE



Waterbird assemblages of inland wetlands in Chile: A meta-analysis

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Abstract

Chile has a large number of wetlands that offer a wide variety of refuges and food to waterbird assemblages. This research hypothesises that these assemblages differ according to the structural characteristics of each type of inland wetland. The object is to identify the structure of these assemblages, evaluating their richness, alpha α diversity and some ecological characteristics, taxonomic structures and trophic guilds. We performed a meta-analysis by submitting pre-selected articles to multivariate reliability analysis. The selected articles were used to characterise the assemblages by alpha α diversity: species richness, Shannon-Wiener index, Pielou's Evenness Index, relative abundance and taxonomic distinctiveness Δ + and beta β diversity: Bray-Curtis with analysis of similarity percentage. Diversity and evenness differed in the seven wetlands studied, among 12 to 45 species, Shannon-Wiener index H'= 0.08 to 0.94 bits and Pielou's Evenness Index J'= 0.06 to 0.71. Four wetlands were below and three above the expected value for taxonomic distinctiveness (Δ +) (73.2 units). Two clusters were identified using the β diversity: one consisting of the High-Andean wetlands (Huasco and Negro Francisco); and the other of El Peral lagoon, the Cruces River wetlands complex and the Tranque San Rafael man-made wetland. The most remarkable dissimilarity was provided by three species (Cygnus melancoryphus, Phoenicoparrus jamesi and Phoenicoparrus andinus). Zoophagous species that eat invertebrates by the first choice are the dominant group, while in lagoon wetlands phytophages and omnivores are more evenly represented.

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Keywords

Birds, diversity, southern Chile, taxonomic distinctiveness

Introduction

Wetlands are defined by the Ramsar Convention (Ramsar 2013) as "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres". Five types of wetlands are recognised: Lacustrine, Riverine, Palustrine, Marine and Estuarine (Dugan 1990; Scott and Jones 1995). Inland wetlands are mainly: (a) Lacustrine (e.g. coastal lagoons, lagoons and lakes), (b) Riverine (e.g. waterfalls, rivers, streams, creeks and floodplains) and (c) Palustrine (e.g. bogs, sedge-marshes, fens, shrub-dominated marshes, swamps, seasonally flooded meadows, sloughs, ñadis and marshes). There are also swamp forests, peatlands and man-made wetlands (e.g. reservoirs, dams). Due to its geographical and bio-climatic characteristics, Chile presents many of these types of wetlands (Dugan 1990; Ramírez et al. 1991; Villagrán and Castro 1997; Schlatter and Schlatter 2004; Squeo et al. 2006; Correa-Araneda et al. 2011; Möller and Muñoz-Pedreros 2014; Cepeda-Pizarro et al. 2016). In some cases they combine spatially to form wetland complexes (e.g. with seasonally inundated areas, bogs, riverbeds and/or lagoons).

Wetlands are ecosystems of great biological alpha α diversity, explained by the multiple levels of biological organisation that coexist there, from the genetic composition of many species of different kingdoms to the diversity of environments, considering the structure, function and composition of the elements of biodiversity and their ecological relations (Noss 1990; Kusler et al. 1994; Gibbs 1995; Barbier et al. 1997; Muñoz-Pedreros and Möller 1997). In these ecological relations, assemblages are groups of taxonomically similar species which use different resources but share some components of the habitat, occupying the same space and time (Fauth et al. 1996; Begon et al. 2006). Thus we recognise that a wetland can contain different assemblages which are ecologically interrelated (e.g. assemblages of waterbirds, fish, arthropods and zooplankton); they are therefore ecologically specialised communities in terms of their feeding and use of the habitat, with specific groupings in different types of wetlands (Siegfried 1976; Kantrud and Stewart 1977; Kauppinen 1995). Characterisation of their feeding habits allows us to study guilds within assemblages (see Jaksic 1981; González-Salazar et al. 2014). Wetlands are structurally complex habitats, in which species find sufficient resources for feeding and sites for reproduction (Schlatter and Sielfeld 2006); they also offer a greater alpha α diversity of microhabitats than other ecosystems.

Schlatter and Sielfeld (2006) define waterbirds as those species that are hatched, live, reproduce, feed and/or perish in wetlands; their presence is therefore strictly associated with humid areas (Scott and Carbonell 1986), including the surround-

ing aquatic vegetation. Our target group was the birds of inland wetlands, however various species of waterbirds associated principally with marine wetlands (e.g. plovers, sandpipers, gulls) also use inland wetlands to feed, rest and even reproduce. Likewise, some inland species may use marine areas during some periods of their life cycle or in some parts of the country. Thus the separation between marine and inland waterbirds is only artificial – especially in some parts of Chile – but it can be used to analyse their diversity (alpha α and beta β), feeding type, use of habitats, etc. (Vilina and Cofré 2006; Vilina et al. 2006).

Birds play important roles in the functioning of these aquatic ecosystems (Martínez 1993), either through their ecological role (e.g., bringing in and consuming nutrients Blanco 1999; seed dispersal Clausen et al. 2002); their value for ecotourism (Klein et al. 1995; Muñoz-Pedreros and Quintana 2010); as bioindicators of environmental changes (Fernández et al. 2005; Amat and Green 2010); or as predators (Gálvez-Bravo and Cassinello 2013). Knowing the structure of a wetland's waterbird assemblage can provide information about its productivity at the different trophic levels, and the particularities of its structure and functioning (Beltzer 1989). Although the importance of waterbirds is recognised, there are great gaps in information about assemblages of this group in inland wetlands (Victoriano et al. 2006).

Structures of waterbird assemblage must be characterized in order to gauge, using different metrics, the species richness and frequencies in each wetland. In addition, the diversity of these ecosystems should also be studied through an analysis of diversity that includes alpha α diversity: species richness, Shannon-Wiener index, Pielou's Evenness Index, relative abundance, and taxonomic distinctiveness Δ +, and beta β diversity: Bray-Curtis with analysis of similarity percentage.

Our working hypothesis was that the diversity (alpha α and beta β), of waterbirds differs in different types of inland wetlands. The object of the study was, through a meta-analysis, to identify the structure of waterbird assemblages in a group of inland wetlands, evaluating their richness, diversity, taxonomic structures and trophic guilds.

Materials and methods

Selection of articles

A meta-analysis allows the results of various studies – related with the object of the analysis – to be combined in order to draw conclusions (Glass 1976). For the present article we considered published information suitable for re-analysis in order to characterise and compare inland waterbird assemblages. The search covered two sources: (a) Bibliographic extraction from Lazo and Silva (1993) and Vega et al. (2011). To complete the information for the years 2012 to 2017, we used (b) Databases, i.e., Scopus, Google Scholar, Center of Environmental and Agrarian Studies Database, using the keywords "waterbirds", "assemblages" and "Chile" (Boolean operators AND; until 10/23/2017). This search produced 414 records of articles published in peer-

Census method	Value
Not described	0
Vaguely described	1
Partially described	2
Completely described	3
Sampling effort	
Single sampling	0
Sampling only in the breeding season	1
Seasonal sampling (at least once in each season)	2
Annual sampling (at least once per month)	3
Description of the study area	
Not described	0
Vaguely described	1
Partially described	2
Completely described	3
Type of journal	
Dissemination	0
With editorial committee	1
Indexed (e.g. Latindex, Biosis, Zoological Records)	2
Mainstream (e.g. Ex ISI, Scopus)	3

Table 1. Factors used to assign Eligibility Value (EV) to the articles found.

reviewed journals. After the literature survey, we decided on articles specifically focused on waterbirds of inland wetlands based on the title and abstract.

We selected articles from this pool by analysing their reliability, using a mathematical algorithm that we developed based on four variables to determine Eligibility Value (EV), namely: (i) Census method used in the article (M); (ii) Sampling effort (E); (iii) Description and precise location of the study area (e.g. geo-referencing, habitat) (D); and (iv) Type of journal (e.g. with or without editorial committee, indexed) in which it was published (R). We considered the most important variables to be the Census method and Sampling effort, so they were assigned a greater weighting than the other two variables. The formula used was:

$$VE = M * 1 + E * 1 + D * 0.5 + R * 0.25$$

The weightings assigned to each variable, according to its importance, are indicated. The values ranged between zero and 9.75 (maximum). Articles awarded \geq 4 points (close to 50%) were selected for analysis. Table 1 shows the weightings used for each variable. The weightings were assigned by a panel of experts.

Birds of Chile's inland wetlands

Schlatter and Sielfeld (2006) recognise 166 species of waterbirds for Chile, with no endemic species, representing 35% of all Chilean bird species. According to Victoriano et al. (2006), excluding the marine ecosystem there are 133 species (29% of the bird species recorded for Chile). For this study we considered waterbirds that inhabit inland wetlands sensu stricto (lacustrine, riverine and palustrine), including species which

have a marked relation with aquatic environments and excluding species which do not need aquatic ecosystems for their everyday habits even if they may be observed in these environments (e.g. members of the family Hirundinidae). We also excluded birds considered rare according to the criterion of Barros et al. (2015), who defines as 'errant' those species with fewer than five recorded sightings per year; this was determined by analysing recorded information from January 2000 to January 2019 in the scientific publications of the search already described, and of the eBird platform, already filtered (eBird.org). Finally, we drew up a list of inland wetland birds following the systems of Barros et al. (2015) and Remsen et al. (2020).

Analysis of ecological diversity

The information extracted from the selected articles was subjected to diversity analysis, including alpha diversity (α), i.e. the diversity of bird species present in each type of wetland, and beta diversity (β), understood as the degree of change or replacement in species composition between the different types of wetland (Whittaker 1972; Whittaker et al. 2001).

The α diversity was measured by species richness (*S*) and the Shannon-Wiener Diversity Index, which quantifies the total diversity of a sample influenced by two basic components, species richness and evenness. The formula for this functio ($pi \times \log_2 pi$), where pi is the proportion of the total number of individuals of the species in question in the sample. The values ranged between zero, when there was only one species, and the maximum (H' max) corresponding to $\log_2 S$. In addition, Pielou's Evenness Index (*J*) was calculated according to the equation: J = H'/H' max (Pielou 1969). This index describes the species evenness of a community, hence it measures the proportion of the observed diversity (*H'*) in relation to the maximum expected diversity (H' max). Its values fluctuate between 0 (minimum heterogeneity) and 1 (maximum heterogeneity, i.e. the species are equally abundant) (Magurran 1998; Magurran and McGill 2011). We processed this test in a programme created by the authors in an Excel spreadsheet. The relative abundance (AB%), understood as the percentage of the total number of individuals (sensu Krebs 1989), allowed us to identify poorly represented species (low abundance).

To describe the degree of taxonomic relation between the species in each site, we calculated the mean taxonomic distinctiveness (Δ +) (Warwick and Clarke 1995, 1998), understood as an intuitive measure of biological diversity since it considers the mean taxonomic breadth of a sample. To do this we used the taxonomic levels: species, genus, family, order and class, following the classification proposed by Remsen et al. (2020). This index evaluates the species richness together with the taxonomic distance between each pair of species, defined using a Linnaean classification tree. The equation used was: $\Delta + = 2 \sum i \neq j \omega i j$ (S – 1), where S is the number of species in the sample and $\omega i j$ is the distinctive weight or taxonomic distance between species *i* and *j* in a taxonomic tree; i.e. each hierarchical level of taxonomy receives a proportional value on a scale of 1 to 100. Thus the value $\omega i j = 20$ indicates the same species, $\omega i j = 40$ is assigned to differ-

ent species of the same genus, $\omega ij=60$ to different genera of the same family, ij=80 to different families of the same order and finally $\omega ij=100$ to different orders of the same class. In other words, the more species belonging to different genera and families there are at a site, the higher the value of Δ + will be, and therefore the higher the diversity.

To analyse the waterbirds beta diversity, the species abundance data were logtransformed (x+1) and generated a Bray-Curtis similarity matrix. Based on similarity hemi-matrices, we obtained an array by non-metric Multidimensional Scaling (MDS) analysis to evaluate and visualise the similarity arrays between sampling points. The similarity-based arrays were also used to generate a cluster analysis between groups, according to the types of environment evaluated. Finally, to identify the species primarily responsible for at least 80% of the bird assemblage structure, we carried out a similarity percentage analysis (SIMPER, Clarke 1993) to quantitatively indicate which birds explain the differences between groups. All the analyses were carried out using the PRIMER-E v6.1.12 software (Clarke and Gorley 2006).

Feeding habits

We grouped the birds into trophic guilds according to their feeding habits, following Martínez (1993): Phytophages (algae and/or macrophytes); Zoophages (invertebrates and/or vertebrates) and Omnivores (phytophagous and zoophagous). Some zoophagous species consume principally invertebrates, and vertebrates only as a second choice (called Ziv); others have plant matter as their second choice (called Zif). Among phytophages, some species consume algae as first choice and macrophytes as second choice (called Fam). Thus the first letter of the code indicates the general classification: zoophagous (Z), phytophagous (F) or omnivorous (O), while the second and third letters indicate the first and second feeding choices (see Martínez 1993) (see Suppl. material 1).

Results

Selection of sources

We identified 22 articles containing information on inland waterbird assemblages in Chile. The Eligibility Value (*EV*) was calculated (Table 2) and 17 were pre-selected (*EV* >4). Seven of these presented meta-data (information suitable for extraction, tabulation and re-analysis) which we could use in our work; the study areas were distributed among four eco-regions of Chile (sensu Dinerstein et al. 1995). In the Atacama Desert eco-region, Salar de Huasco (Sielfeld et al. 1996) and Laguna Negro Francisco (Oyarzo and Correa 1991); in the Chilean Matorral eco-region, Tranque San Rafael dam (Egli and Aguirre 1995) and Laguna El Peral (Riveros et al. 1981); in the Valdivian Rain Forest eco-region, the wetlands complexes of Lago Lanalhue (Muñoz-Pedreros and Merino 2014) and Río Cruces (Morales and Varela 1985);

Source	М	S	D	Т	EV
Aguirre et al. (2007)	2	4	2	1	7,25
Egli and Aguirre (1995)	3	4	3	1	8,75
Garay et al. (1991)	3	4	3	3	9,25
González-Acuña et al. (2004)	3	4	3	1	8,75
González-Gajardo et al. (2009)	3	1	3	3	6,25
Ibarra et al. (2010)	3	4	3	3	9,25
Ibarra et al. (2009)	3	3	3	3	8,25
Kusch et al. (2008)	3	3	3	0	7,5
Meza (1986)	2	1	1	0	3,5
Meza et al. (1999)	2	4	3	0	7,5
Morales and Varela (1985)	3	4	3	0	8,5
Muñoz-Pedreros and Merino (2014)	3	4	3	3	9,25
Oyarzo and Correa (1991)	2	1	3	0	4,5
Rau (1983)	1	3	1	1	4,75
Riveros et al. (1981)	3	4	3	1	8,75
Schlatter (1976)	1	0	3	1	2,75
Sielfeld et al. (1996)	2	3	3	1	6,75
Simeone et al. (2008)	3	4	3	1	8,75
Tabilo et al. (2001)	2	4	1	1	6,75
Tabilo (2006)	0	0	3	1	1,75
Torres-Mura and Lemus (1991)	1	1	3	1	3,75

Table 2. Eligibility Value (EV) of the publications analysed. M: census method, S: sampling effort, D: description of the study area and T: type of journal.

and in the Sub-polar *Nothofagus* Forest with Patagonian Steppe eco-region, Laguna de Los Cisnes (Rau 1983). These wetlands fall into four ecosystem types: two High-Andean wetlands (Negro Francisco and Huasco), one man-made wetland (Tranque San Rafael), two wetlands complexes (Río Cruces and Lago Lanalhue) and two lagoon (El Peral and Los Cisnes).

Birds of inland wetlands

The list of inland wetland birds consisted of 113 species, as shown in Suppl. material 1; the orders with the greatest representation are the typically aquatic orders like Charadriiformes with 31 species (27.4%), followed by the Anseriformes with 29 species (25.6%). The order Passeriformes presented 15 species (13.2%), more than some exclusively aquatic orders like Gruiformes (10.6%), Pelecaniformes (8.8%), Podicipediformes (4.4%), Phoenicopteriformes (2.6%), Ciconiformes (1.7%) and Suliformes (1.7%). The least represented orders are the Accipitriformes (1.7%), Strigiformes (0.8%) and Coraciformes (0.8%), which consist of species related with aquatic environments only by their feeding habits.

Alpha diversity

In the seven sites studied 72 species were recorded (Table 3, Suppl. material 2), with species richness ranging between 12 and 45 species (Table 4). The species richness gradient of the wetlands is as follows: the greatest species richness ($S \ge 30$) was found

in the Río Cruces complex and Tranque San Rafael; medium species richness ($S \le 29 \ge 19$) was recorded in the Lago Lanalhue complex and Laguna El Peral; and low species richness ($S \le 18$) in the High-Andean wetlands of Negro Francisco and Huasco, and in Laguna de Los Cisnes (Table 4). When the species richness of each site is compared by wetland area, it is interesting to see that the richest wetlands are the smallest (Tranque San Rafael, 1 ha) and the largest (Río Cruces complex, >300,000 ha).

The wetlands presented medium to high evenness values (H' ≥ 0.58 , J ≥ 0.50), except for the Lago Lanalhue complex (H' < 0.1; J<0.1) where there was strongly dominant abundance of *C. melancoryphus* (97.7%). The man-made wetland (Tranque San Rafael), which presented the greatest species richness (and the smallest area) also presents high evenness, similar to that of the Río Cruces complex, making it the most diverse of the wetlands studied. Both the High-Andean wetland sites have low species richness and medium/high evenness; their similarity is probably explained by the fact that they are high-altitude ecosystems influenced by similar environmental variables.

		NDEAN ANDS	MAN-MADE WETLAND	WETLANDS COMPLEX		LAGOON	
Locality	Huasco	Negro Fran- cisco	Tranque San Rafael	Lago Lanalhue	Río Cruces	El Peral	Los Cisnes
Type of wetland	Brackish lagoon and bofedal	Brackish lagoon, bofedal and vega	Dam	Wetlands complexes	Wetlands complexes	Lagoon	Lagoon
Location	Iquique	Atacama	Metropolitana	Biobío	Valdivia	Valparaíso	Punta Arenas
Coordinates	20°15.00'S, 68°50.00'E	27°26.00'S, 69°15.00'E	33°16.00'S, 70°53.00'E	37°55.00'S, 73°17.00'E	39°42.00'S, 73°12.00'E	33°30.00'S, 71°36.00'E	51°01.00'S, 72°52.00'E
Altitude (masl)	3,800	4,200	498	12	0	9	206
Area (ha)	6,000	1,200	1	3,100	341,407	20	12
Source	Sielfeld et al. 1996	Oyarzo and Correa 1991	Egli and Agu- irre 1995	Muñoz- Pedreros and Merino 2014	Morales and Varela 1985	Riveros et al. 1981	Rau 1983

Table 3. Characterisation of seven inland wetlands in Chile.

Table 4. α diversity in four types of wetlands in Chile. S= species richness, H'= Shannon-Wiener Index. H'max.= Max. value of Shannon-Wiener Index. J= Pielou's evenness index. Δ + = Mean taxonomic distinctiveness.

	HIGH-AND LAN		MAN-MADE WETLAND	WETLANDS	COMPLEX	LAG	NOC
-	Huasco	Negro Francisco	Tranque San Rafael	Lago Lanalhue	Río Cruces	LagunaEl Peral	Laguna de Los Cisnes
S	14 (12.3%)	17 (15%)	45 (39.8%)	20 (17.6%)	30 (26.5%)	19 (16.8)	12 (10.6%)
H' (bits)	0.58	0.63	0.94	0.08	0.94	0.82	0.77
H'max (bits)	1.15	1.23	1.54	1.30	1.48	1.28	1.08
J'	0.50	0.52	0.61	0.06	0.63	0.64	0.71
Δ + value	74.07	74.56	71.54	71.68	74.94	69.82	56.67

Beta diversity

The β diversity is medium, since the majority of the wetlands (five out of seven) present a similarity greater than 55% and less than 65%; the only sites that are clearly dissimilar are Los Cisnes and the Lago Lanalhue wetlands complex (<35% similarity) (Fig. 1). Two clusters are observed with more than 50% similarity, one consisting of the High-Andean wetlands (64.4% similarity) and the other of Tranque San Rafael, Río Cruces and El Peral (55.8% similarity) (Fig. 2). Similarity percentage analysis (SIMPER) indicates that the greatest contributions to the dissimilarities between the wetlands derive from the species *C. melancoryphus*, *P. jamesi* and *P. andinus* (Table 5); these species present the greatest frequencies in the counts, and between them explain more than 50% of the dissimilarity between the assemblages (Table 5). This explains why the high dissimilarity of the Lago Lanalhue complex is dictated by the high presence of *C. melancoryphus*.

The expected value for taxonomic distinctiveness (Δ +) was 73.2 units. Four wetlands were below this value (Los Cisnes, lago Lanalhue, Tranque San Rafael, El Peral) but within the funnel plot (which expresses the 95% confidence interval). Los Cisnes presented a Δ + value of 56.67 units, putting it outside the funnel plot, i.e. the weight of the branches of its Linnaean tree is low, meaning that the species that make up this assemblage present lower phylogenetic diversity. The High-Andean wetlands (Negro Francisco and Salar de Huasco) and the Río Cruces wetlands complex were above the expected value; the latter in particular is at the upper limit of the plot with a Δ + of 74.94 units (Fig. 3), implying that its diversity is the highest of all the sites.

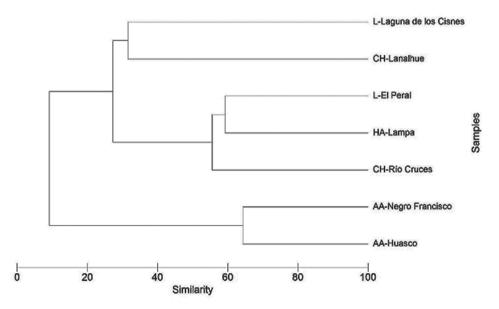


Figure 1. Bray-Curtis similarity tree diagram of the wetlands analysed. AA= High-Andean wetlands (Huasco and Negro Francisco), HA= man-made wetland (Tranque San Rafael), CH= wetland complexes (Lago Lanalhue and Río Cruces), L= Lakes (El Peral, Los Cines).

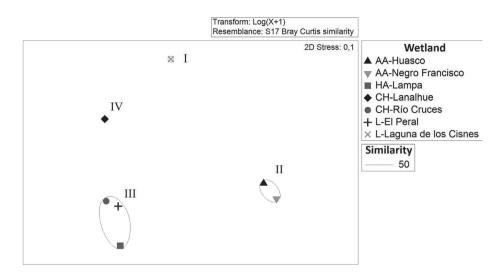


Figure 2. Multidimensional ordering (MDS) of the composition and abundance of bird species between seven wetlands (Stress: 0.12) based on the Bray-Curtis similarity index. Ellipses and numbers show groups with 50% similarity. AA= High-Andean wetlands (Huasco and Negro Francisco), HA= man-made wetland (Tranque San Rafael), CH= wetland complexes (Lago Lanalhue and Río Cruces), L= Lagoon (El Peral, Los Cisnes).

Table 5. Analysis of the percentage contribution of species to dissimilarity (SIMPER).

Species	Contrib. %	Cumulative %	
Cygnus melancoryphus	19.14	19.14	
Phoenicoparrus jamesi	17.68	36.82	
Phoenicoparrus andinus	14.86	51.68	
Anas georgica	9.811	61.49	
Fulica armillata	8.242	69.73	
Fulica leucoptera	5.379	75.11	
Leucophaeus pipixcan	4.073	79.19	
Phoenicopterus chilensis	3.279	82.46	

Feeding habits

Seventy-two species of inland waterbirds (64%) are zoophagous (Z); 93% of these consume invertebrates by first choice (Zi), while just five zoophagous species prefer to consume vertebrates (Zv); 22% are omnivorous species (O), of which 72% are phytophagous by first choice (Of); finally, 14% are strictly phytophagous species (F) (see Suppl. material 1). In the High-Andean wetlands, the majority of species are zoophagous (>50%) consuming principally invertebrates (Zi); other zoophagous species consume vertebrates by second choice (Ziv). These groups belong to the families: Recurvirostridae, Charadriidae, Scolopacidae and Laridae. Two phytophagous species (Fa) were also recorded which consume algae (diatoms and unicellular algae), *P. andinus* and *P. jamesi*; they are the only species with this feeding pattern in the assemblages studied.

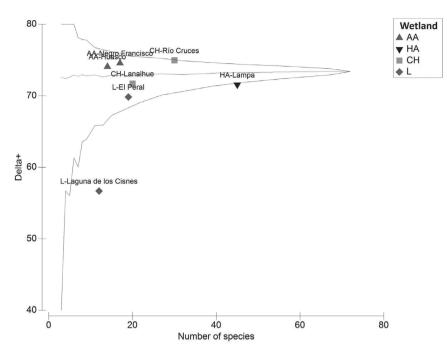


Figure 3. Funnel plot of the mean taxonomic distinctiveness (Δ +) of seven inland wetlands in Chile. AA= High-Andean wetlands (Huasco and Negro Francisco), HA= man-made wetland (Tranque San Rafael), CH= wetland complexes (Lago Lanalhue and Río Cruces), L= Lagoon (El Peral, Los Cisnes). Expresses 95% confidence interval.

The man-made wetland Tranque San Rafael presented the largest number of trophic guilds (eight), followed by the wetland complexes and the High-Andean wetlands (seven), Los Cisnes Lagoon (six) and El Peral Lagoon(four). The zoophagous species that consume invertebrates by preference form the majority (>50%) in the wetlands complexes, and in man-made and High-Andean wetlands, while in lagoons more even proportions are found between zoophagous, phytophagous and omnivo-rous species (Fig. 4).

Discussion

Diversity

The seven wetlands studied are in different eco-regions (sensu Dinerstein et al. 1995), two in the Atacama Desert eco-region; two in the Chilean Matorral eco-region; two in the Valdivian Rain Forest eco-region; and one in the Sub-polar *Nothofagus* Forest with Patagonian Steppe eco-region. On the other hand, they are different types of wetlands, two High-Andean wetlands, one man-made wetland, two wetlands complexes and two lagoons.

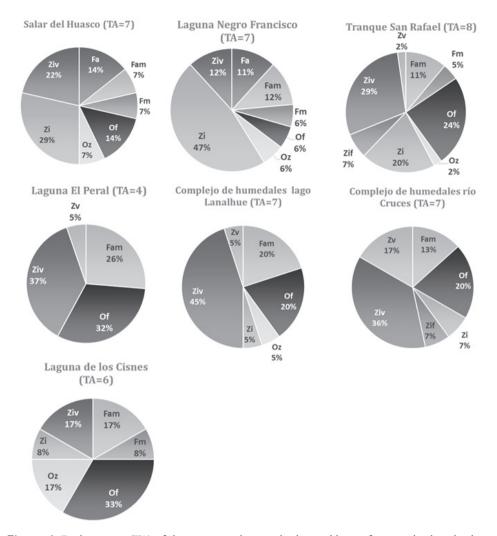


Figure 4. Feeding types (TA) of the species in the waterbird assemblages of seven inland wetlands in Chile. Z= Zoophagous (i= principally invertebrates; v= principally vertebrates). F=Phytophagous (a= principally algae; m= principally macrophytes). O= Omnivorous (f= principally phytophagous; z= principally zoophagous) (Martínez 1993).

To explain the alpha α diversity in the wetlands analysed, we can speculate that the differences between them are linked to the availability of habitats and to productivity: spatial heterogeneity and a dense food supply allow greater trophic specialisation, and thus the presence of a larger number of bird species (Pianka 2000). The authors of the articles analysed did not carry out studies of microhabitats or of food supply; we therefore propose that differences in the species richness (and abundance) of species may be linked to these two factors, without excluding the degree of human intervention (a variable which was likewise not studied). This would suggest that greater alpha α diver-

sity of species would be observed in more pristine environments; however the wetland with the greatest species richness is the man-made wetland, Tranque San Rafael, which also presents the largest number of trophic guilds.

When we analyse the seven wetlands selected, classified into four types, we deduce that the most structurally complex environments do not necessarily harbour a larger number of species, since the diversity of the ecosystem is also subject to the stability and singularity of the habitats to provide the necessary conditions and sustain a determined number of species (see Levey 1988; Wiens 1989; Ball and Nudds 1989; Poulin et al. 1993; Ronchi-Virgolini et al. 2013; Tavares et al. 2015; Lorenzón et al. 2016; Quiroga et al. 2021). For example, in the Río Cruces and Lago Lanalhue wetlands complexes, differences were found in the structures of the assemblages, despite the fact that both are environments with high spatial heterogeneity and low anthropic intervention. This may be explained by the high frequency of the species *C. melancoryphus* recorded in Lago Lanalhue (mean 2,200 individuals), resulting in low evenness; this species migrated from Río Cruces in 2004 when the latter was impacted by a cellulose plant (see Jaramillo et al. 2007; Muñoz-Pedreros and Merino 2014).

Perspectives for the study of waterbird assemblages

Wetland ecosystems have been rapidly altered and reduced by human activities (Wilen 1989; Gibbs 2000). Wetlands of different origins, such as natural (Dugan 1990), urban (González-Gajardo et al. 2009) and even agricultural (Czech and Parsons 2002), are recognised as important environments for waterbirds. Conservation and/or management of these ecosystems is therefore indispensable. Many of Chile's wetlands are not inside protected areas and are subject to strong pressure by economic activities such as extraction of natural resources and un-programmed and uncontrolled tourism activities (Muñoz-Pedreros and Möller 1997; Schlatter et al. 2001; Möller and Muñoz-Pedreros 2014). Knowledge of the structure of bird assemblages can help us to understand how wetlands function, and this information can be used in the generation of conservation and management plans and programmes.

There are very few studies of inland waterbird assemblages in Chile, and there are many sites of great importance whose structure and diversity have not been analysed. Of the wetlands studied, three are Ramsar sites: Salar de Huasco, Laguna Negro Francisco and Río Cruces (Carlos Anwandter Sanctuary), but the other 13 have few studies, like other priority wetlands (e.g., Elqui river mouth in the Atacama Desert eco-region, Rocuant-Andalíen marsh and Chamiza wetlands in the Valdivian Rain Forest eco-region). This lack of information hinders the development of proper conservation strategies and programmes for the waterbird assemblages present in inland wetlands. Of the 17 articles pre-selected, only seven presented meta-data (information suitable for re-analysis); it is therefore vitally necessary to establish a more demanding protocol for information-gathering which includes the presentation of meta-data, to allow integral, standardised analysis. At the same time, specific indices and methodologies should be applied to the analysis of biological diversity (e.g. α diversity, β diversity, γ diversity;

focal species; fine, medium and coarse filter analysis); functional factors should also be included, and their relation with habitat characteristics. It is important to consider the uses of these indices because the well documented patterns of spatial and temporal variation in diversity continue to stimulate the minds of ecologists today. On the other hand, measures of diversity are frequently seen as indicators of the wellbeing of ecological systems (sensu Magurran 1998).

The diversity consists of not one but two components: the variety and the relative abundance of species, and the indices consider these two aspects. Species richness may only be one component of diversity but it is relatively simple to measure, yet species diversity measures (indices) are often more informative than species counts alone. In the environmental monitoring, diversity measures are widely used and have been extensively tested and prove that diversity measures can be empirically useful (Magurran 1998). All this information would allow the development of a large monitoring program, which together with interconnected citizen science initiatives (e.g., eBird) also contribute to efficient planning of waterfowl conservation.

It is important to explore the need to integrate a type of functional traits among others into the analysis of biological diversity like ecology of feeding. Community studies of inland waterbirds could focus on the guild composition of taxonomic assemblages (see Jaksic 1981; Jaksic and Medel 1990), not simply on species composition, since this provides greater clarity on ecological processes; consideration of the guilds in waterbird assemblages is essential for understanding the role of guilds in the organisation of wetland communities (e.g. Hoeinghaus et al. 2007; Kissling et al. 2011; González-Salazar et al. 2014). All this would allow conservation decisions to be taken based on scientific criteria. The e-Bird bases do not cover the target wetlands. In the future, these citizen records may be used. For now, a meta-analysis based on published studies is one of the best ways to document waterbird assemblages in Chile.

Author's contributions

MLM and AMP contributed to the conception and design of the study. AM performed the literature search and/or organised the database. HVN produced the figures and/or tables. MLM and AMP wrote the first draft of the manuscript. AMP and HVN wrote sections of the manuscript. Authors reviewed and/or analysed the literature and contributed to manuscript revision, read, and approved the submitted version.

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Supplementary material I

Supplementary material 1

Authors: María L. Miranda-García, Andrés Muñoz-Pedreros, Heraldo V. Norambuena Data type: docx file

- Explanation note: Birds of Chile's inland wetlands. Status: P= Species present, NR= Non-breeding, E= Errant (sensu Barros et al. 2015). Feeding: Z= Zoophagous (i= principally invertebrates; v= principally vertebrates). P=Phytophagous (a= principally algae; m= principally macrophytes). O= Omnivorous (p= principally phytophagous; z= principally zoophagous) (sensu Martínez 1993). F = Phytophagous (a = mainly algae; m = mainly macrophytes).
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- Link: https://doi.org/10.3897/natureconservation.45.74062.suppl1

Supplementary material 2

Supplementary material 2

Authors: María L. Miranda-García, Andrés Muñoz-Pedreros, Heraldo V. Norambuena Data type: docx file

- Explanation note: Frequency and abundance of waterbirds in seven inland wetlands in Chile.
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